A new Middle Devonian heterocoral from Spain

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Most of the heterocorals described up to now from strata older than Famennian are of doubtful affinities. Numerous specimens of the new genus and new species here described were collected during a sedimentological study of the Santa Lucía Formation in La Pola de Gordon (León province, Cantabrian Mountains, NW Spain). *Stellaphyllia luciensis* gen. et sp. nov. is characterized by cylindrical coralla, with a diameter of less than 2 mm and more than 2 cm long, having stellate to more or less rounded outer profile. Four to six septa, less frequently seven, are cojoined axially by a short oblique septum. The few tabulae present are steeply arched. The microstructure of the septa and interseptal elements shows thin elongate microlamellae parallel to a median plate which is granular in appearance. The new genus dated to the lower Eifelian age could be important in understanding the early phylogeny and origin of the order Heterocorallia.

Key words: Heterocorallia, Eifelian, Cantabrian Zone, Spain.

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Introduction

The Heterocorallia were long thought to be restricted to strata of Visean age (Weyer 1967). Following the classical works of Różkowska (1968, 1969), and papers by Weyer (1990, 1995a, b), many heterocorals have been recorded from the Famennian of Poland, Germany and Morocco. However, older occurrences remain somewhat doubtful (Weyer 1991; Wrzołek 1993; Nudds and Sepkoski 1993). Thus, typical heterocorals described in this paper from the lower Eifelian of North-Western Spain are of great interest for understanding of the origin and evolution of the order.

The specimens described in this paper are housed in the Department of Geology (Paleontology section), University of Oviedo (Spain), abbreviated DPO. The material consists of four thin sections and one ultra-thin section with catalogue numbers DPO 15440 to DPO 15444. Each of the four thin sections contains several heterocorals sections, which are labeled with a number added to the DPO number.

Supposed occurrences of Heterocorallia in the Middle Devonian

Pseudopetraia Soshkina, 1951, *Tetraphyllia* Yoh, Jin, Zhen, and Xie, 1984, and *Mariaephyllia* Fedorowski, 1991 are the only pre-Famennian heterocorals described until now. Nevertheless, most of them are of doubtful affinities.

Hill (1981) claimed to recognize a heterocorallian pattern in the septal disposition of *Pseudopetraia* Soshkina, 1951 and she tentatively suggested that the genus belonged in the order Heterocorallia Schindewolf, 1941. The type species of *Pseudopetraia*, *P. devonica* Soshkina comes from the Emsian of the Pokrovskoe village in the Egorshinskiy region, on the eastern slopes of the Middle Ural Mountains (Soshkina 1951; Weyer 1991). The type material of this species was redescribed and illustrated by Fedorowski (1991: figs. 24–25). The stratigraphy of this occurrence was discussed in detail by Weyer (1991). This last author described a new species assigned to *Pseudopetraia*, *P. issa* Weyer, 1991, from the middle Pragian of the Bergär Sattel in the Eastern Thuringian Shaly Massif. He studied in detail— through the preparation of serial sections—the ontogeny and septal insertion of this species. Dicussing the affinities of the genus itself, he convincingly demonstrated that it is not related to the Heterocorallia *sensu stricto*.

A new genus represented by a new species was described as *Tetraphyllia devonica* by Yoh et al. (1984), from the upper Emsian of Gumu, in the Wenshan country of the Yunnan province in Southern China. It was thought to belong to a new family, Tetraphylliidae, of the order Heterocorallia. This species was discussed by Fedorowski (1991) and by Weyer (1991). Both authors recognized that the descriptions and illustrations by Yoh et al. (1984) were insufficient to understand the true affinities of this organism. But Fedorowski (1991)

agreed with a heterocorallian interpretation and even created a new suborder, Tetraphyllina Fedorowski, 1991, probably at the base of the Heterocorallia clade and including *Tetraphyllia*, *Oligophylloides* Różkowska, 1969, and *Mariaephyllia* Fedorowski, 1991. The position of Weyer (1991) is radically different: according to him, nothing in the description or poor illustrations demonstrates the heterocorallian affinity of *Tetraphyllia devonica* and he proposed classifying it as "*incertae sedis* (Anthozoa?)". The authors agree with this proposition and consider it impossible to decide on the correct assignment of this organism given the information currently available, although a heterocorallian interpretation was reaffirmed by Lin et al. (1995).

Recently, Glinski (1998) assigned to the genus *Mariaephyllia* a new species, *M. eifeliensis*, coming from the Eifelian of the Eifel Hills (Germany). His material comes from one sample and contains some thirty sections. We agree that most of the figured sections (Glinski 1998: fig. 1a–h, pl. 1: 2, 3) probably represent true heterocorals, but coral sectioned and chosen by the author as a holotype of *M. eifeliensis* (Glinski 1998: pl. 1: 1) seems to us to be of doubtful affinity (perhaps Rugosa or Bryozoa?).

Thus and up to now, *Mariaephyllia eifeliensis* is the only representative of Heterocorallia *sensu stricto* whose presence before the Famennian has been convincingly demonstrated.

Geographical and stratigraphical setting of the Spanish occurrence

The only sample containing heterocorals from Spain was collected by R. Herrmann (Freies Universität Berlin) from an outcrop of the Lower to Middle Devonian Santa Lucía Formation, near the small village of Geras de Gordón, west of La Pola de Gordón (Bernesga Valley, southern slope of the Cantabrian Zone, NW Spain) (Fig. 1).

The Santa Lucía Formation is composed of shallow marine limestones in which reefal facies are common. This formation has been studied from a sedimentological and paleontological point of view by several authors: Coo (1974), Méndez-Bedia (1976), Herrmann (1990), Fernández-Martínez (1994), Méndez-Bedia et al. (1994), Soto et al. (1994) and Herrmann and Hubmann (1994), among others. According to most of these authors, carbonate facies in this formation are arranged in parallel strips with subtidal facies towards the west and southwest, and shallower water, both lagoonal and peritidal deposits, towards the east, where an emerged area, the so called Asturian High, was located. This arrangement, in addition to the presence of bioclastic (crinoidal) carbonate sand bars interpreted as open marine facies in the most southern outcrops, suggests the deposition of these limestones as having taken place on a carbonate platform. Nevertheless, Herrmann (1990) and Herrmann and Hubmann (1994) disagree with this sedimentological model and suggest that the sediments of the Santa Lucía Formation were deposited on a gently southwardly inclined carbonate ramp rather than on a carbonate platform.

The succession of the Santa Lucía Formation at Geras de Gordón, where the studied sample came from, is shown in Fig. 2. A detailed description of this succession can be found in Herrmann and Hubmann (1994). In this section and near the top of the formation, some irregular and laterally impersistent thin grainstone beds are intercalated with clayey layers. The grainstones beds are mainly formed by crinoidal and sometimes by bryozoan debris. The studied sample was taken from a 10 cm thick brown clayey layer, placed about 4 m below the top of the formation. This layer yielded a rich fauna of fenestellid and delicate branching bryozoans, crinoids, small ramose tabulate corals and, in at least one of the samples, heterocorals.

The thin sections containing heterocorals consist of a bryozoan packstone, locally grainstone, with numerous, highly packed, debris of brachiopods, crinoids, corals, trilobites and calcareous spicules. Some erosive contact between debris, secondary growth of calcite and silica, secondary dolomitization in organic cavities and iron oxides are also present in these samples. The organisms in the packstone layers are extraordinarily well preserved with respect to their internal structure and their completeness, and thus they can be regarded as autochtonous and parautochtonous. Sedimentary structures are not recorded, probably because of the strong compaction as a consequence of the high clay content.

The occurrence of delicate, fragile organisms (bryozoans, tabulate corals, heterocorals), the fine grain size of the surrounding sediment and the often complete preservation of fragile organisms point to quiet conditions with only a little water movement. Nonetheless water circulation and nutrient supply were good enough to allow the growth of a rich benthic epifauna. Occasionally stronger water movements caused the deposition of the grainstone layers which buried the bryozoan/coral assemblage. Similar assemblages with bryozoans and small tabulate corals (*Bainbridgia* assemblage) are known from other places (Tourneur 1991): Bainbridge Limestone, Missouri, USA; Hamar Laghdad Kess-Kess, Tafilalt, Morocco; Chynice Vapence, Barrandian, Czech Republic; Greifensteiner Kalk, Rheinish Slate Mountains, Germany; among others, and they are usually interpreted as representing some deep or low energy environments.

Several associations of conodonts representing the *P. costatus costatus* Zone have been identified from bioclastic bars at the top of the Santa Lucía Formation in some outcrops near Geras de Gordon (Buggish et al. 1982; García-López 1987). As the sample which yielded heterocorals was taken from a layer 4 meters below the top of this formation, a lower Eifelian age for these organisms could be assumed.

Systematic descriptions

Because of the unknown pattern of septal insertion, heterocorals are a problematic group. After several models of

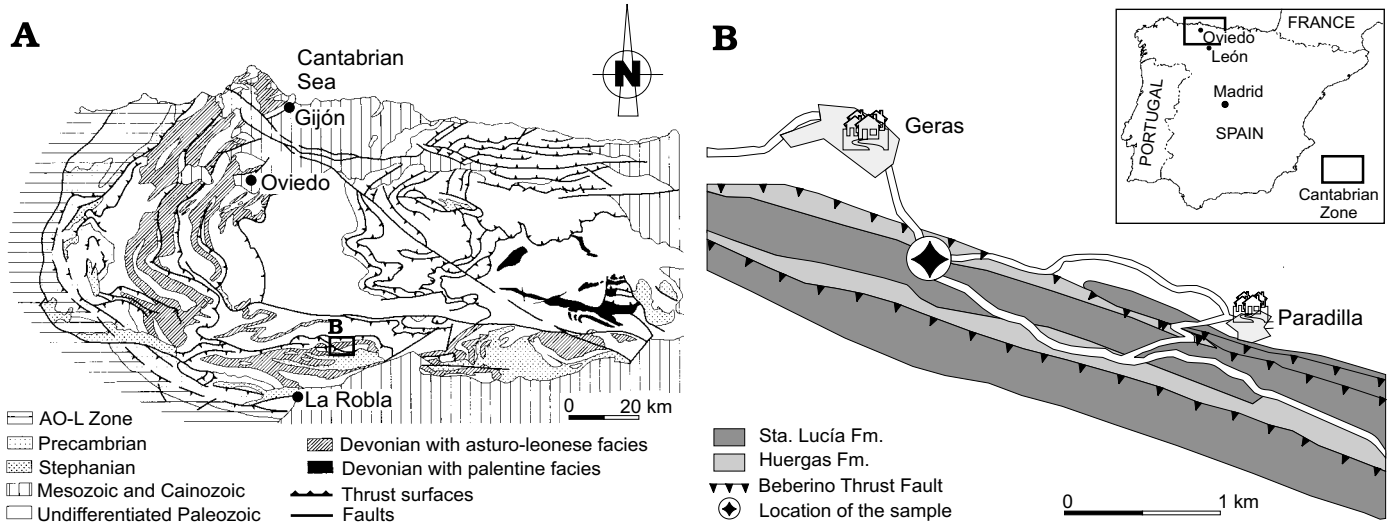

Fig. 1. Geographic and geologic setting of the sample location. **A**. Simplified geology map of Cantabrian Mountains, NW Spain showing position of studied area. AO-L Zone indicates Westerasturian-leonese Zone ("Zona AsturOccidental-leonesa") and the rest of the figure belong to the Cantabrian Zone **B**. Detailed location of the outcrop.

septogenesis related with the rugosan pattern were suggested (Schindewolf 1941; Poty 1978), Fedorowski (1991) proposed a new model featured by the first development of an "oblique septum" (previously pointed out by Lafuste 1979) and further septal growth by splitting of its both ends. According to this model, Fedorowski created a new subclass Dividocorallia, consisting of two orders: the Heterocorallia (Dividocorallia lacking calices) and Calyxocorallia (Dividocorallia possessing calices). Fedorowski's pattern has recently been rejected by some authors (Lin et al. 1995) but most workers in the field agree that growth occurs via division of septal peripheral ends and no accurate new model for septal insertion has been proposed since Fedorowski's work until now. This problem, and the fact that the vast majority of studied specimens are sectioned or incomplete, hampers the systematic description of heterocorals, especially at the familial and generic level, and as a result remains poorly understood.

Subclass Dividocorallia Fedorowski, 1991

Diagnosis.—Anthozoa possessing septa developed due to peripheral dichotomic division; the process starts from a single oblique septum, located axially and inserted at a basal disc.

Order Heterocorallia Schindewolf, 1941

Diagnosis.—Dividocorallia without calices (see Wrzołek 1993: fig. 1E, F, for an illustrated reconstruction of the order).

Family ?Heterophyllidae Dybowski, 1873

The diagnosis below is partially based on Hill (1981), and includes information based on the understanding of Fedorowski's (1991) model of septogenesis.

Diagnosis.—Elongate coralla with no epitheca present and, in their initial stages, comprising four septa conjoined axially, with new septa formed by peripheral division of the previous septa. Tabulae are complete, ranging in form from domes with steeply sloping to vertical, and confluent edges forming layered wall.

Genus *Stellaphyllia* nov. Fernández Martínez and Tourneur

Type species: *Stellaphyllia luciensis* gen. et sp. nov.

Derivation of the name: With reference to the stellate external profile of some specimens.

Diagnosis.—Heterophyllidae with between four and six, occasionally up to seven, septa at the corallite periphery, with thickened septal edges. Sections taken from young specimens, or from near the distal end of mature coralla show a stellate outer profile. Tabulotheca is strongly developed in the mature specimens. Microstructure of septa and interseptal elements composed of microlamellar tissue enveloping granular median plates.

Remarks.—*Hexaphyllia* Stuckenberg, 1904 is a genus which was originally diagnosed by the presence of only six septa, and by a thick peripheral stereozone. It has often been regarded in the literature as an early stage of long *Heterophyllia.* Poty (1978) established the generic status of this form, but some sections possessing six septa can also be considered early stages of other genera. In addition, Rodríguez and Comas-Rengifo (1988–89) described as *Hexaphyllia*? cf. *mirabilis* a population of heterocorals from the Carboniferous of Spain which exhibits a wide range of morphological variations, including a septal number which ranges between four and nine. A sound revision of this genus is therefore necessary in order to establish its true status and diagnostic features.

Our material differs from all the specimens previously assigned to *Hexaphyllia,* not so much for their septal number, but rather because of the comparative thickness of both the

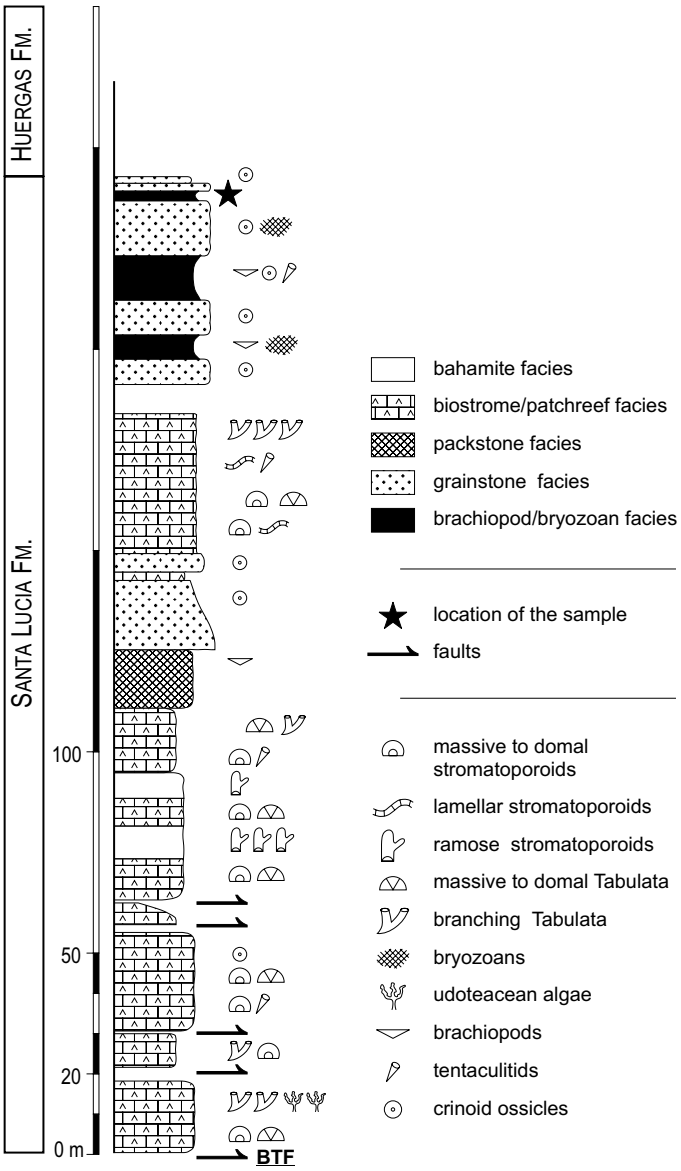

Fig. 2. Stratigraphic column of the Santa Lucia Formation, near Geras de Gordón (the lowest part of this formation is lacking in this section). The sample with heterocorals was taken from the bed marked with a star. Modified from Tourneur et al. (1995).

septal (stellate profiles) and tabular (rounded profiles) sclerenchyme, and thus for their strongly stellate profile, or in their scarcity of interseptal loculi.

Stellaphyllia luciensis gen. et sp. nov. Fernández-Martínez and Tourneur

Figs. 3–10. Table 1.

Derivation of the name: With reference to the Santa Lucia Formation, from where the material originates.

Holotype: Specimen DPO 15440-11 (Figs. 3, 4R, 9F).

Paratypes: Specimens DPO 15440-4 (Figs. 3, 4N, 9D), DPO 15440-5 (Figs. 3, 4H, 9B), DPO 15442-23 (Figs. 3, 4K), DPO 15442-40 (Figs. 3, 4D, 8C) (transverse sections) and DPO 15443-16 (longitudinal section).

Type locality: Geras de Gordón (west of La Pola De Gordón, Bernesga Valley, southern slope of the Cantabrian Zone, in NW Spain) (Fig. 1).

Type horizon: A brown clayey bryozoan packstone. It is placed about 4 meters below the top of the formation (Fig. 2).

Material.—Four thin sections (DPO 15440 to 15443), comprising a total of 44 corallite sections, of which 20 are transverse, 21 vary from being slightly to highly oblique and three are longitudinal. One ultra-thin section (DPO 15444) contains several corallites.

Diagnosis.—Cylindrical coralla, from one to two millimeters in diameter, with four to six, more unusually seven, septa joined axially by an oblique septum. In young specimens and in the sections made very near the top of the mature coralla, only septal thickenings are present, and the outer profile is stellate. In mature specimens, very thick tabulothecal walls are developed.

Methods.—Due to the scarcity of material, it has not been possible to carry out work on ontogenesis with acetate peels and all the specimens described in this paper have been identified through the study of thin sections alone.

In spite of the limited data available, a quantitative study has been carried out which presents observations on transverse or slightly tangential sections only (longitudinal and strongly oblique profiles were omitted from the study) corresponding to three elements:

(1) Corallite diameter. Because the irregular profile of some sections, the diameter was measured along the minimum (not medium) transverse dimension of the corallite.

(2) Septal number. The different proposed models of septogenesis result in several different methods for measuring septal number. In this study, it was determined by counting the number of septa intersecting the external wall in the cross section of a corallite.

(3) The outer profile of the studied cross sections.

Using the data obtained from the measurements of these three features it was possible to perform a simple statistical analysis, which demonstrates the relationships between each pair of features (Table 1 and Fig. 3).

Description and interpretation

Transverse and slightly oblique sections: The main features (diameter, septal number and outer profile) of some selected transverse and slightly oblique sections are shown in Table 1.

Minimum diameter ranges between 1 and 2.1 mm (see Table 1 and Fig. 3).

Septal number usually ranges between four and six, and only one instance with seven septa was observed. As is shown in Fig. 4, the septal configuration varies widely even if only corallites with four septa are considered. Most septa are conjoined axially by an oblique septum (Figs. 4, 8, 9), the length of which seems to increase with the septal number although it can also be absent in some cases.

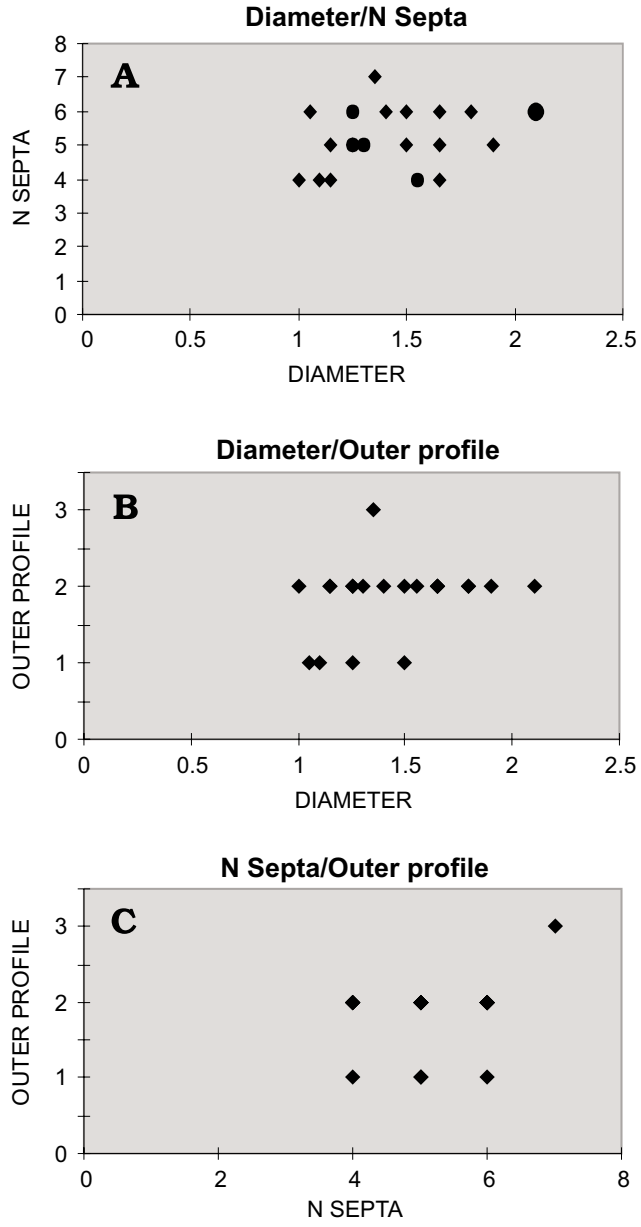

Fig. 3. Correlation of three pairs of parameters. **A**. Diameter (in mm) *versus* number of septa; big circle indicates the holotype; smalls circles are the paratypes. **B**. Diameter (in mm) *versus* outline of the sections (1, stellate profile; 2, rounded profile; 3, oblique section). **C**. Number of septa *versus* outer profile (same legend).

Table 1. Measurements of sections studied. N, sample number (sample with ** is the holotype; samples with * are the paratypes); Dmin, minimum section diameter (in mm); NS, number of septa (counting the number of septa intersecting the external wall in the cross section of the corallite); OP, outer profile of samples studied (star: stellate profile; circle: rounded profile; square: oblique section).

N	Dmin	NS	OP
1	1.8	6	●
2	1.65	6	●
4*	**1.25**	**6**	●
5*	**1.25**	**5**	★
11**	**2.1**	**6**	●
12	1.9	5	●
20	1.5	6	●
21	1.35	7	■
23*	**1.3**	**5**	●
24	1.25	5	●
27	1.05	6	★
28	1	4	●
29	1.15	5	●
31	1.1	4	★
32	1.65	5	●
33	1.65	4	●
34	1.8	6	●
37	1.4	6	●
38	1.5	5	★
40*	**1.55**	**4**	●
41	1.15	4	●

According to Fedorowski (1991), the development of a heterocoral from its basal disc starts with the appearance of a single oblique septum. In the material studied, however, no section could be attributed to this stage. This oblique septum would generate four more septa, through the bifurcation of its extremities, a stage which can be clearly seen in sample DPO 15443-41 (Fig. 4B). However, in several corallites with four septa, either the septa form a cross or the point of union (oblique septum) is rather short (samples DPO15442-40, Fig. 4D, DPO 15442-31, Fig. 4F, and DPO 15442-33, Fig. 4A). This fact indicates the disappearance, whether temporary, partial or total, of the oblique septum, as Fedorowski previously explained (1991). It remains the case that in early ontogenetic stages, the oblique septum appears to be smaller than normal.

On the other hand, one specimen (DPO 15440-13, not figured in this paper) has four septa of some length, and a bifurcation is present in all of its extremities, well developed in one case and less pronounced in the remaining three. The presence of this type of section supports Fedorowski's model of septogenesis (1991) which claims the peripheral division of individual creative septum. However, this specimen would suggest that the subsequent increase in the number of septa is generated by the division of the extremities of the original four large septa that were produced (Fedorowski's "first generation" 1991). Nevertheless, the logical consequence of this system of division would be the generation of eight peripheral septa, a number which none of the corallites studied display (except in the case of one sample, which was in a phase of division).

Thirteen sections with five septa (Fig. 4G–L) were also studied. These occurrences (around 62% of the studied sections) suggest that the habitual development following the four septa stage is the division of just one septum. As can be deduced from the observations made so far, this division could occur in any of the septa. Of the thirteen sections studied, two have small oblique septa (samples DPO 15442-24, Fig. 4I and DPO 15441-42, not figured), but the rest display

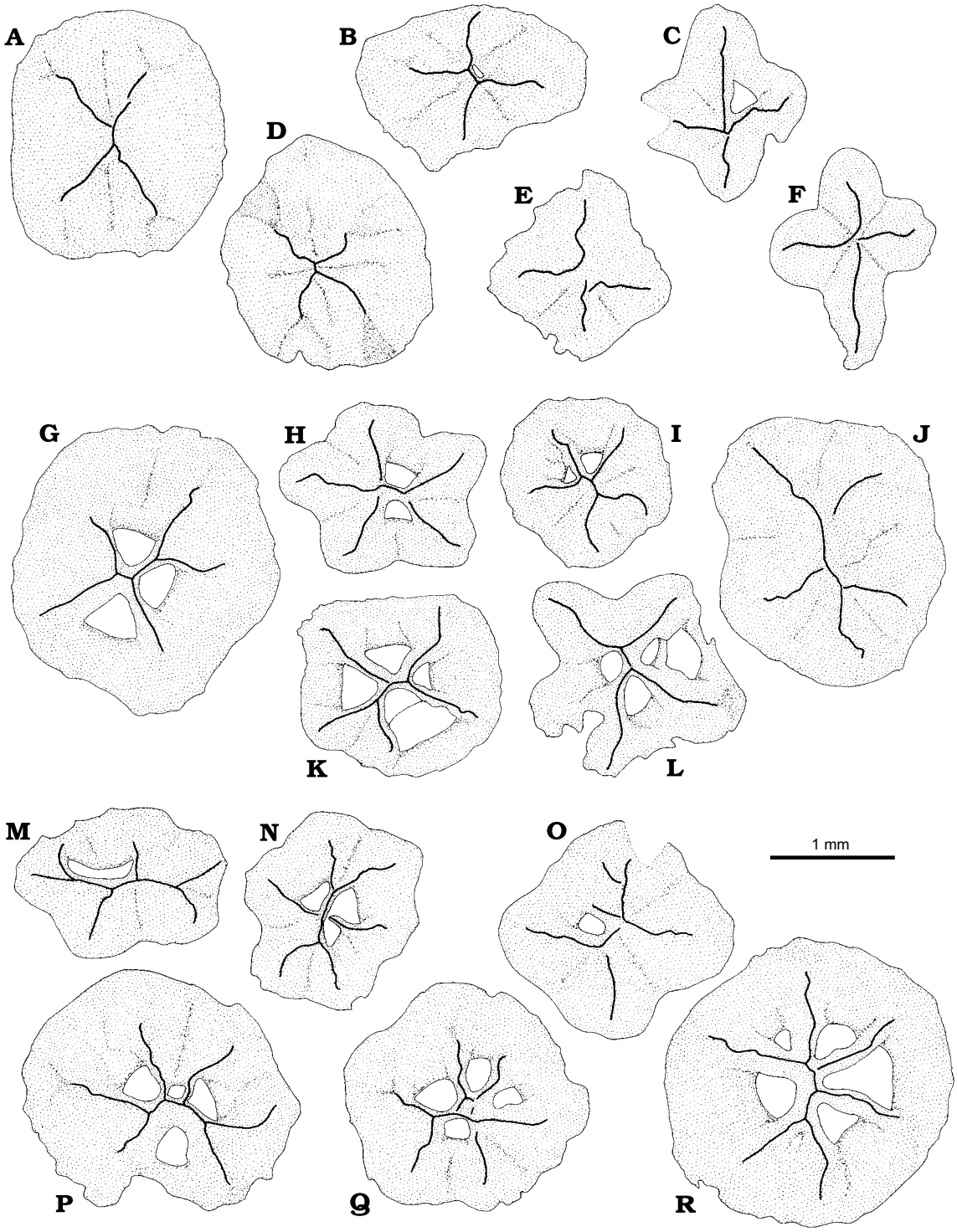

Fig. 4. Schematic drawings of some of the sections studied, grouped according to the number of septa. Note the different sizes and outlines that can be found within each group. In the drawings, the septa can be distinguished by their dark midlines. Upper part (four septa): Specimens DPO 15442-33 (**A**), DPO 15442-41 (**B**), DPO 15440-8 (**C**), DPO 15442-40, paratype (**D**), DPO 15442-28 (**E**), and DPO 15442-31 (**F**). Middle part (five septa): Specimens DPO 15440-12 (**G**), DPO 15440-5, paratype (**H**), DPO 15442-24 (**I**), DPO 15442-32 (**J**), DPO 15442-23, paratype (**K**), 15442-38 (**L**). Lower part (six septa): Specimens DPO 15442-27 (**M**), DPO 15440-4, paratype (**N**), DPO 15442-37 (**O**), DPO 15442-34 (**P**), DPO 15442-27 (**Q**), and DPO 15440-11, holotype (**R**).

septa, which are joined by an ample septal segment (samples DPO 15440-5, Fig. 4H, and DPO 15442-23, Fig. 4K, for example), thus indicating a possible ontogenetic increase in the size of the oblique septum.

Nine sections are with six septa (Fig. 4M–R). Of these, only one (sample DPO 15440-9, not figured) is clearly symmetrical. In the others, the position of the septa varies (as can be seen from a comparison of specimens DPO 15440-11, Fig.

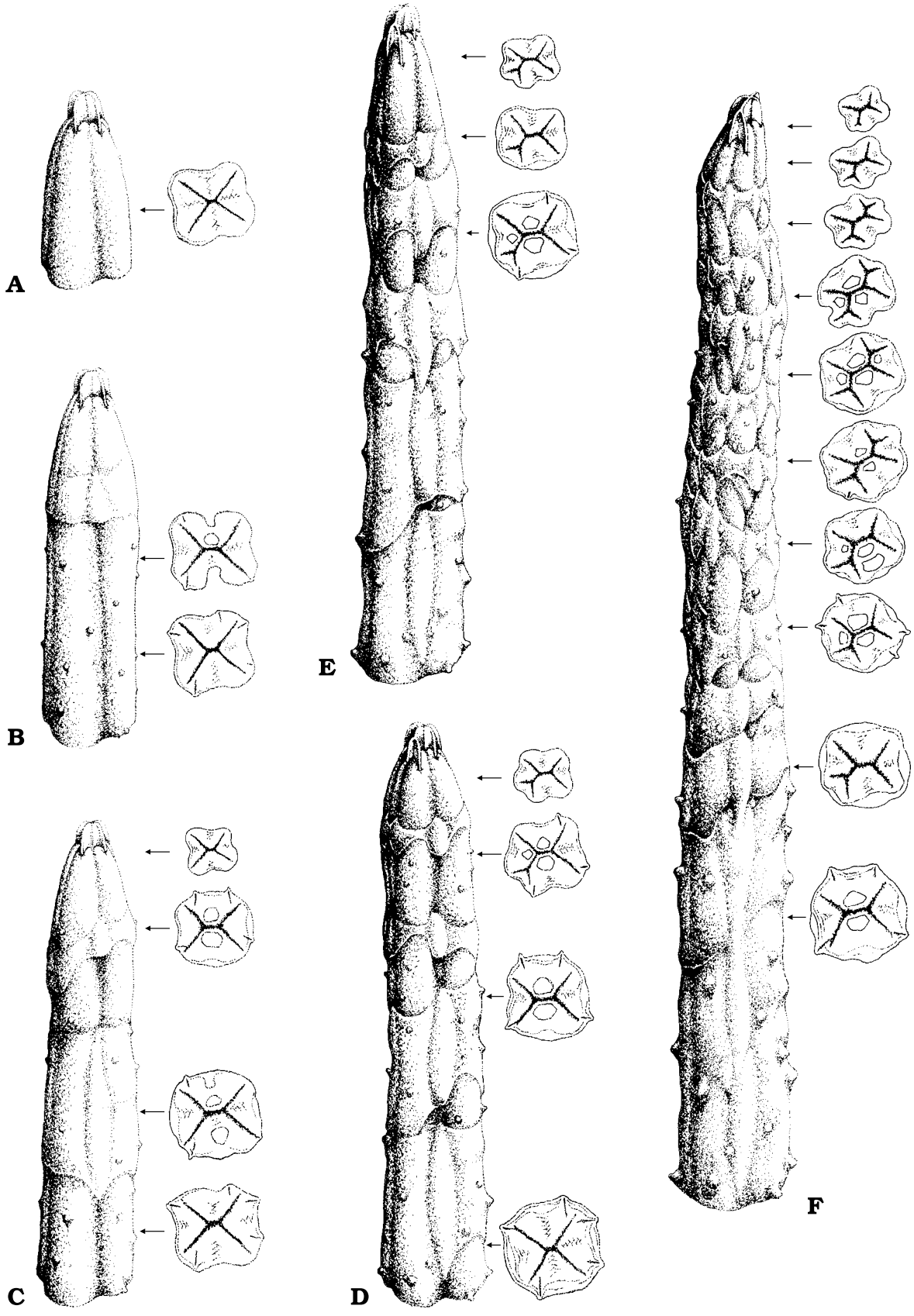

Fig. 5. Reconstruction of the skeletal development of *Stellaphyllia* gen. nov. based on the model of growth put forward in this paper, showing the different sections as they correspond to different ontogenetic stages. **A** to **F** correspond to series of reconstructed growth stages of a solitary corallite (not to scale).

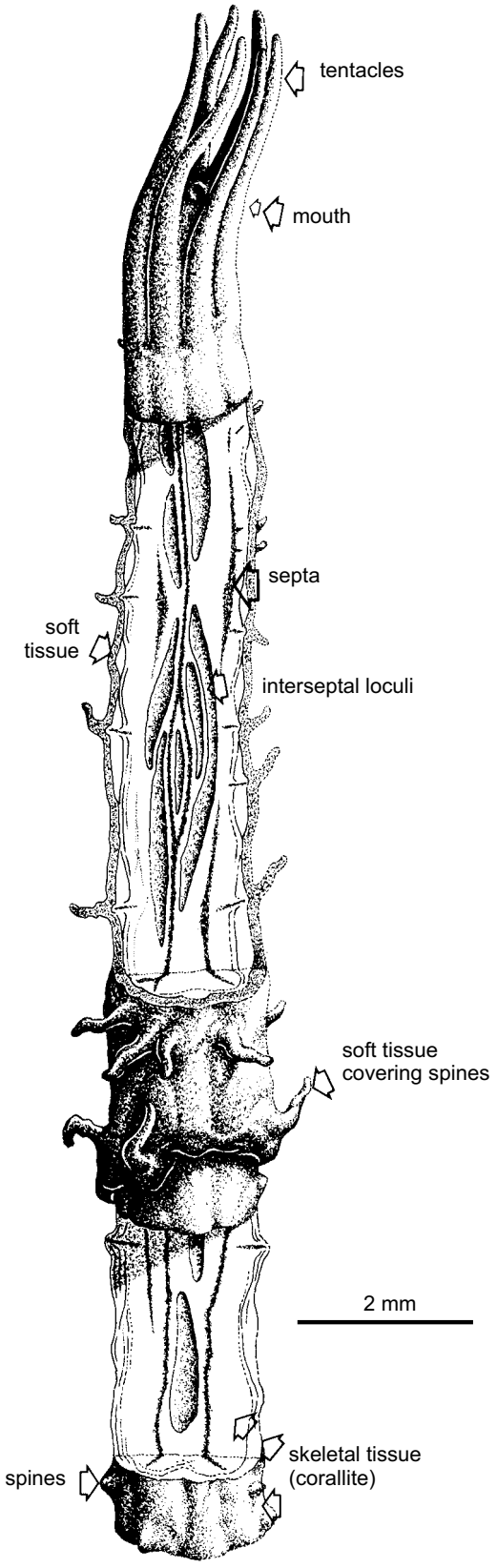

Fig. 6. Suggested reconstruction of *Stellaphyllia* gen. nov. based on the model put forward in this paper. The drawing shows the kind of longitudinal section such as we have observed in our material. Soft tissue of the polyp (denser stipple on the surface) is supposed on the basis of the hard skeletal tissue and on the scleractinian polyps.

4R and DPO 15440-12, Fig. 4G), but all of them show a septal segment of certain length which could be, or not, attributed to the original oblique septum. Lack of ontogenesis studies prevents a suitable interpretation of these observations.

Only one section with seven septa (sample DPO 15442-21, not figured) has been observed. If septogenesis is accepted as being the result of the peripheral division of individual creative septa, the seventh septum must have come from the extreme periphery of one of the septa from the previous generation, which would have needed a lengthening of the coral in the direction of the creative septum. Indeed, this section has a rounded, but slightly elongated, outline.

Sample DPO 15440-9 (not figured) has eight septa, but, judging from its appearance, it is a corallite in a stage of division and thus could be assigned to two different individuals.

The detailed observation of the sections previously described demonstrates the wide variety of positions and arrangements of the septa. This fact supports the ideas of Fedorowski (1991) and Sugiyama (1997) that the four original septa produced by the oblique septum have the same creative potential. In several cases, free septa have been observed, whose appearance was explained by Fedorowski (1991). No septa with thickened peripheral endings of their midlines have been observed among the studied sections, where the distal ends of the septa are not free but integrated into the external wall of the coralla (tabulotheca). Those specimens which show their septa reaching the peripheral part of the coralla are either broken, or have been sectioned very obliquely (Fig. 8F for instance).

Coralla can display either a stellate (eight sections) or a rounded (ten sections) outer profile (Figs. 3, 4, 8, 9, and Table 1). Stellate outer profiles are generated by the wide ridges of the septa and thus the septal number is similar to the number of ridges (for example, Figs. 8F, 9B). Three of the eight sections studied consist of four ridges (that is, four septa); four sections consist of five ridges; and only one section consists of six ridges. In each case, the middle zone of the ridge coincides with a septal median line whose peripheral edge does not reach the most external part of the corallum (see Fig. 9B for a good example). The other ten specimens studied in cross section have rounded profiles (see, for instance, Figs. 8C, 9C, F).

The thickness of the septal and tabulothecal sclerenchyme is related to the outer profile. Owing to the similarity in microstructural composition of both sclerenchymes, in only a few cases has it been possible to distinguish between them in the material studied. Only very detailed observation of the microstructural elements has facilitated the identification of the septal sclerenchyme in the areas surrounding empty zones (interseptal loculi), and also in some compact (lacking interseptal loculi) specimens. In the specimens displaying stellate outer profiles, the presence of septal but not mural (tabulothecal) thickening, cannot be dismissed. The rounded profile is produced by the development of short interseptal walls between the wide septal ridges.

Two types of interseptal loculi have been identified. The first consists of an "empty" zone, bordered by two septa and

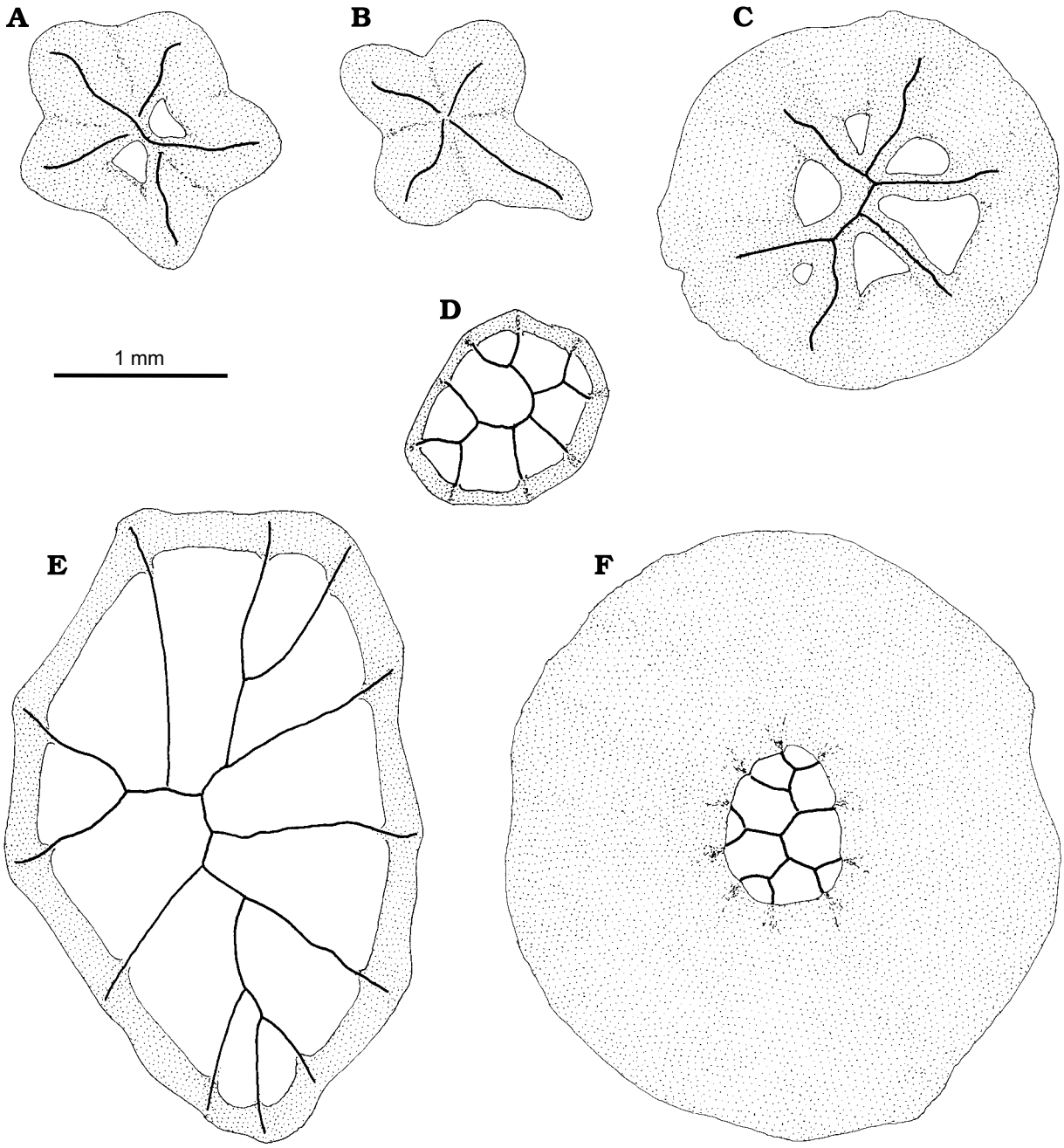

Fig. 7. Comparison of morphology of *Stellaphyllia* gen. nov. (**A**–**C**), with *Mariaephyllia* (**D**) from the Fammenian of Poland, and *Heterophyllia* (**E**), and *Oligophylloides* (**F**), both from the Visean of Belgium.

the inner edge of the tabulotheca; a zone which is diagenetically filled with irregular calcite crystals, often with very poorly defined limits (Figs. 4, 8F, 9A–D, F). In the vast majority of specimens, these "empty" zones are found near the oblique septa and increase in size towards the periphery. The number of these zones in one specimen ranges from zero to six. Only one tabula is normally present in each loculum, although in three exceptional cases, two tabulae have been observed (Fig. 4K, L)

In six sections showing both stellate and rounded profiles, each interseptal area is totally, or almost totally, filled by the sclerenchyme (Figs. 4, 8B, C, E, G, among others). In these cases, a dark zigzag line usually appears in the middle part of the area, and can be interpreted as the limit between zones with differently oriented microstructural elements.

Interpretation according to the transverse sections: If the previously established models of Fedorowski (1991) and Sugiyama (1997) are accepted, then a clear relationship should exist between the size of the coralla, the number of septa and the external profile. In this way, an increase in the number of septa should create a corresponding increase in overall size, and a rounding off effect on the external profile.

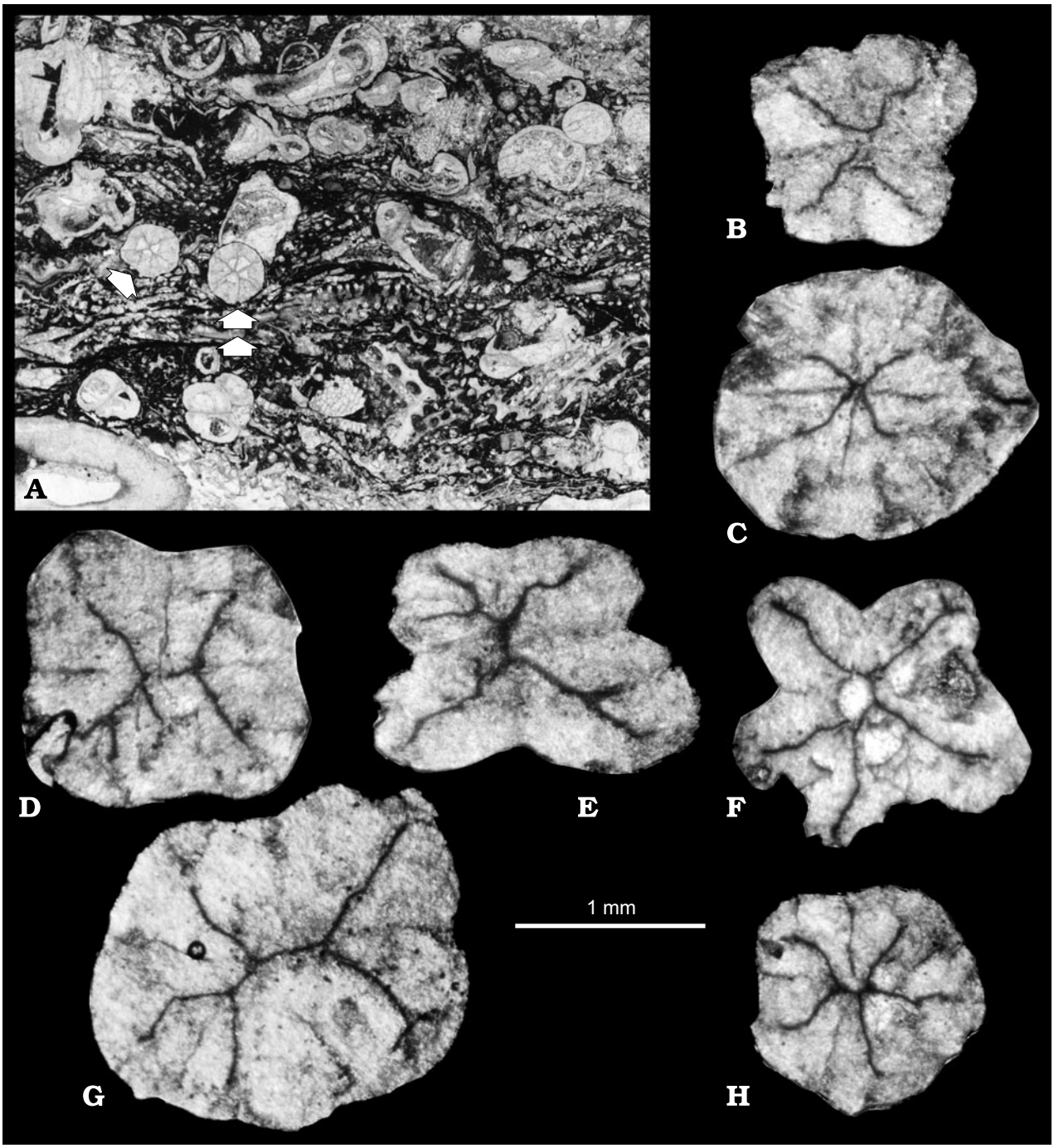

Fig. 8. *Stellaphyllia luciensis* gen. et sp. nov. Morphology. **A**. General view of a fragment of the thin section DPO 15440 containing two cross sections of heterocorals (white arrows), the holotype is marked with two arrows; × 4.5. **B**. Transverse section of DPO 15442-28, with four septa and a profile in the process of rounding-off. **C**. Transverse section of DPO 15442-40, with 4 septa and a rounded outline. **D**. Transverse section of DPO 15442-37, with four septa. Note that one of the septa is in the beginning of a bifurcation. **E**. Transverse section of DPO 15442-25. Note the stellate profile of the section and the presence of four septa, two of which are bifurcated. **F**. Specimen DPO 15442-38. Transverse section with five septa and a stellate profile. **G**. Transverse section of DPO 15442-32, with five septa and a slightly rounded profile. **H**. Specimen DPO 15442-24. Transverse section of a corallum with five septa and a markedly rounded outline.

However, the studied sections demonstrate no clear relationship between these factors (Figs. 3, 4, 6 and Table 1).

Roughly, it could be said that the coralla with six septa are generally big and rounded, a fact which fits in with all previous models of heterocoral growth. However, as can be seen in the correlation charts, there is no obvious factor which links an increase in the number of septa (ontogenetic growth) with an increase in the size of the corallum or the degree of roundedness. Thus, there are sections with four septa which are small with a stellate profile (samples DPO 15442-31, Fig.

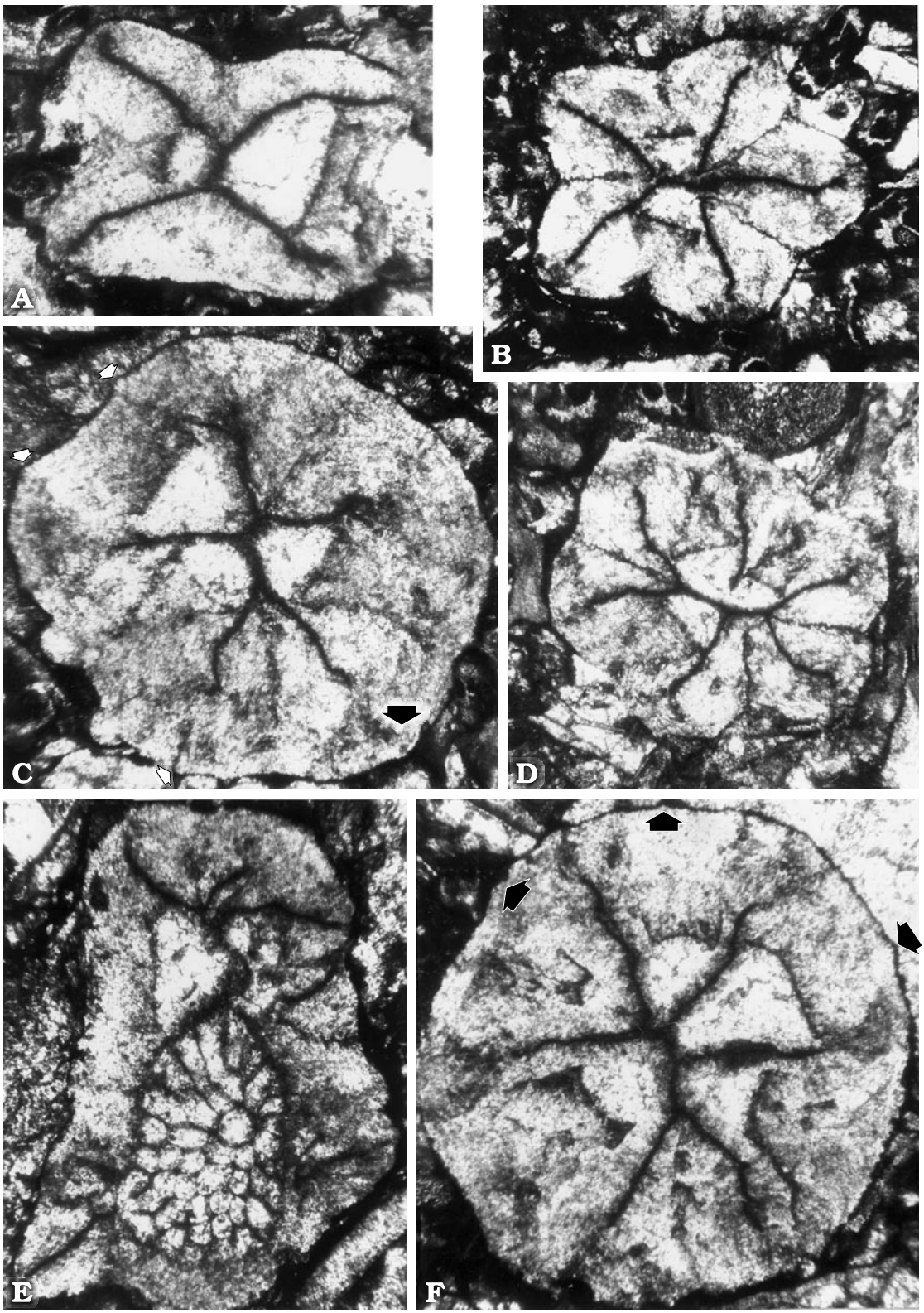

Fig. 9. *Stellaphyllia luciensis* gen. et sp. nov. Morphology. **A**. Specimen DPO 15440-3, cross-section (slightly oblique) with a stellate profile and four septa. **B**. Transverse section of DPO 15440-5. Note the stellate profile generated by the strong development of sclerenchyme. **C**. Transverse section of DPO 15440-12, with five septa and a rounded profile. Arrows point to the small granules over the external surface of the coralla. **D**. Transverse section of DPO 15440-4, DPO 15440-4, with six septa and a slightly stellate profile. **E**. Specimen DPO 15440-14. A cross section showing a heterocoral growing around a branching bryozoan. **F**. Transverse section of the specimen DPO 15440-11. Holotype. Cross section with a rounded profile, six septa and four interseptal loculi. Arrows point to three small granules over the external surface. All × 35.

4F, and DPO 15440-8, Fig. 4C), others which although rounded, are of small or medium size (DPO 15442-33, Fig. 4A and DPO 15442-40, Figs. 4D, 8C), and still others with six septa which are small and slightly stellate (DPO 15440-4, Fig. 4N and DPO 15442-37, Fig. 4O), although the majority of those with six septa are large and rounded.

It is possible that this lack of correlation is due to the small size of the sample, but commenting on the same phenomenon, Rodríguez and Comas-Rengifo (1988–89) also noted the absence of correlation between the thickness of the wall and other characteristics such as the diameter, or the number of septa, in a sample of more than 700 specimens. Thus, other explanations should not be dismissed.

Any explanation for this ausence of coherence with previous models should take into account three unquestionable facts: (1) The increase in the number of septa, from four to six, and more rarely to seven, during the ontogenetic development of the coralla. (2) The sections described belong to both different ontogenetic stages and different specimens. (3) The centrifugal mode of growth of Heterocorallia; in fact, according to Wrzołek (1981, 1993), Fedorowski (1991) and Cossey (1997): "it now seems likely than in all heterocoral genera the tabulae curve peripherally downwards away from the corallite axis before fusing to form the corallite wall" (Cossey 1997: 1040, 2text-fig. 3A). Thus, and for the specimens described in this paper, it can be assumed that both the final size and the degree of roundness are not only the result of an increase in the area occupied by the septa, but also of the thickness of successive tabulae covering the indentations in the stellate forms and adding sclerenchyme to the septal ridges.

Bearing these three facts in mind, it is possible to interpret the more rounded shapes as corresponding to sections from the lower part of the corallum where, regardless of the ontogenetic stage displayed, there is a more significant secondary sclerenchyme growth. For the same reason, the stellate forms can be interpreted as corresponding to the sections taken near the tip of the corallum, whether in young specimens of four septa or in mature coralla with five or six septa (Fig. 5). This interpretation supports the presence, on the top of the corallum, of a distal cone just as Wrzołek (1981, 1993) and Karwowski and Wrzołek (1987) deduced from the study of the genus *Oligophylloides*. Unfortunately, no section from this hypotethical structure has been observed in the Spanish material and thus, we have drawn the distal cone after the previously mentioned model.

Longitudinal sections: Only three longitudinal sections, more or less oblique, are present in the material studied. Two aspect of morphology can be seen clearly in these sections. In some examples, one or more septa longitudinally sectioned appear as well defined black lines (Fig. 6). Their course is mildly wavy rather than straight, although some fragments show more irregular arrangements. Septa which are regularly joined to others have also been observed. In all the sections, but especially in one of them (DPO 15440-43), dark areas with diffuse and irregular outlines can be seen (Fig. 6). In our opinion, this is due to very oblique sections crossing the interior of the septa.

The second element to be observed is the scarce presence of steeply oblique to almost vertical tabulae (Fig. 6). In some cases, the presence of an area filled by the sclerenchyme of thick walls (tabulotheca) has been noted between two consecutive, vertical tabulae (that is, the top of one tabulae forms the base of the next). It would be possible to conclude that the total or partial absence of interseptal loculi in some cross sections is actually due to the sections having been cut precisely where those zones were located.

Although it could be an effect of the sections studied, there are several instances of clear asymmetry among the tabulae observed on either side of any septum. Thus, on one side of a given septum there is an empty space, whilst on the other side of the same septum, an area filled with wall esclerenchyme (tabulotheca) can be found. Sections thus characterised by the joint presence of empty interseptal areas, and interseptal areas filled with wall sclerenchyme could be the result of the cutting process mentioned previously.

The fact that, in the same section, the area between the septa can be either empty or full of wall sclerenchyme implies that the surface of the wall at any given moment is not of a uniform height throughout the corallum, and can vary. In fact, as the longitudinal sections indicate, their heights do vary in different interseptal sections.

In some cases, the presence of zones with walls showing a different appearance is evident. This feature could be the result of diagenesis and fragmentation of the specimens, or it could reflect a microstructural difference between the outer wall of the tabulotheca and the septal sclerenchyme.

Likewise, where the wall appears to be well preserved, there are small granules- or spines-like projections, which correspond to trabeculae ending within the sclerenchyme. According to some observations, it is thought that these spines were generated at the terminal parts of some septa (Figs. 4A, 9C). The transformation from granular to fibrous tissue is not uncommon among the Palaeozoic corals (Lafuste et al. 1992, among others). In one of the specimens studied, unfortunately a badly preserved one, the presence of variously arranged small cavities can be observed, which could be the result of stress undergone by the polyp at a certain moment.

Microstructure: The microstructure (Fig. 10A, B), examined on one ultra-thin section, shows septal median plates composed of small, uniformly sized granules which do not change during the septal development but some of them develop a fibrous end which generates a spine (Fig. 9F).

The interseptal parts are microstructurally homogeneous and they are composed of long microlamellae which are only slightly bent towards the exterior of the corallite (Fig. 10B), clearly indicating the abaxial direction of the skeletal secretion. Some concavities are also developed on the exterior or concave side of each microlamella. The microlamellae are 3–5 μm high and 18–27 μm long (Fig. 10B). Tabulae are also composed of microlamellae but their bases are underlined by a thin layer of granules. The microlamellae display a concordant arrangement within a

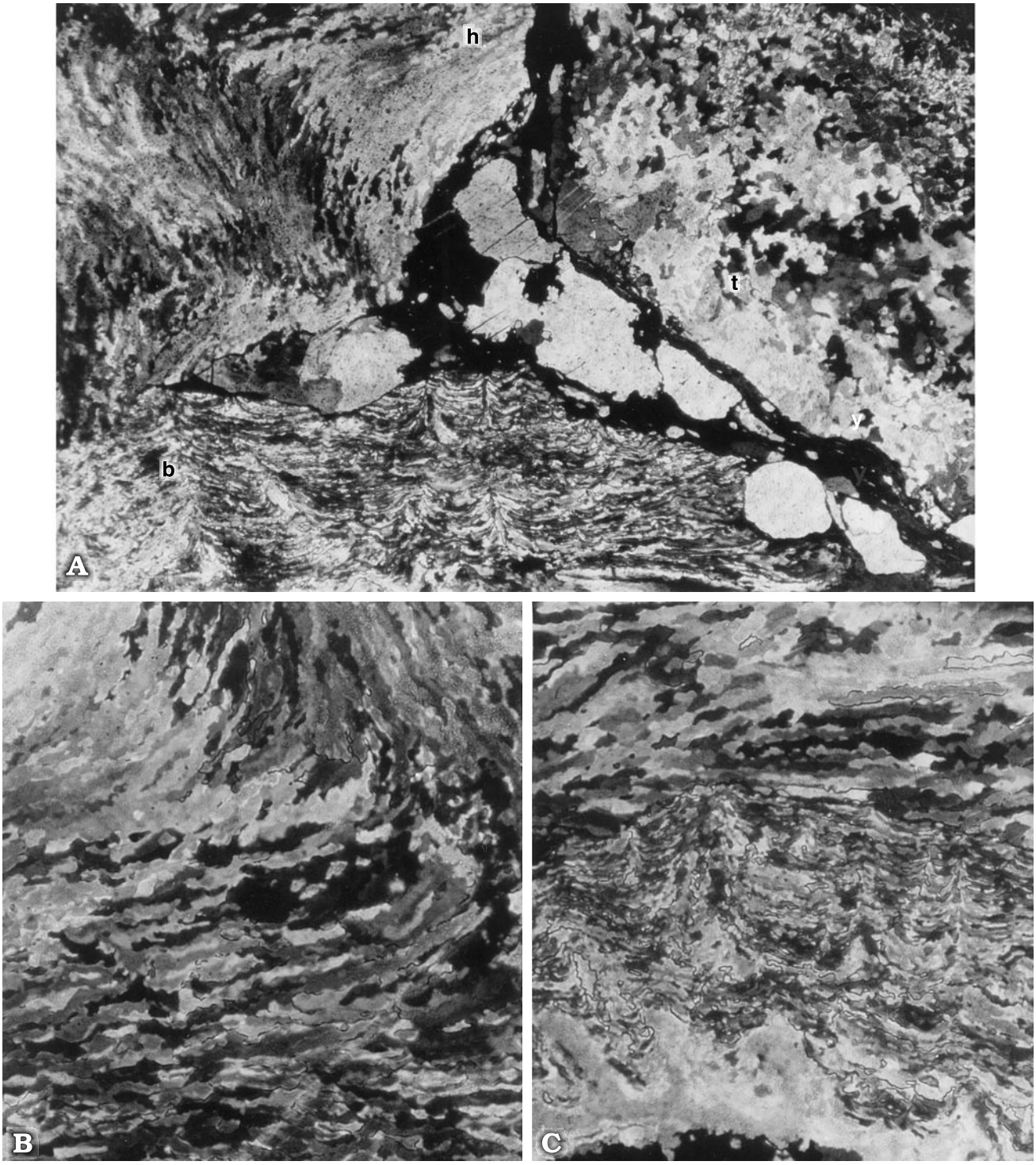

Fig. 10. *Stellaphyllia luciensis* gen. et sp. nov. Microstructure. DPO15.444. **A**. Occurrence of three different organisms in the same ultra-thin section: *Stellaphyllia luciensis* in transverse stellate section (h, top left), a larger transverse section of striatoporid tabulate coral (t, top right) and a small fragment of fenestellid bryozoan (b, bottom). Note the three different microstructures: extended microlamellae disposed in a large regular curve in *Stellaphyllia*, short and thick microllamellae arranged on both sides of narrow granular median plates in the tabulate coral, and very thin lamellae with a regular wavy pattern of the bryozoan; × 220. **B**. Detail of the microstructure of *Stellaphyllia luciensis* gen. et sp. nov.: extended, rather thin microlamellae with cupular surface showing the same orientation of the cupules concavity towards growth direction of the skeleton; microlamellae are disposed in regular conformity; colour change in the lower left part corresponds to a change in the orientation of these microelements; × 450. **C**. Detail of the contact between a bryozoan in the lower part and an auloporid tabulate coral in the upper part. The bryozoan shows a microstructure composed of very thin lamellae lacking a clear cupulosity, disposed in a regular undulating pattern with each peak axed by a spiny trabecular structure. On the other hand, the auloporid tabulate shows a microstructure composed of larger and thicker lamellar elements than the bryozoan; × 450.

septum and thus, they are parallel to septal flanks and curved around the septal margins. This disposition forces a change in the general orientation, with a corresponding change in the colour of the skeletal mass (due to the change in the orientation of the C axis of the calcite crystals) and the development of a fine, dark, zigzag line as an effect of the refringence (Fig. 10A).

The finely laminated structure of *Stellaphyllia luciensis* sp. nov. is comparable with that of the Famennian genus *Oligophylloides* Różkowska, described by Karwowski and Wrzołek (1987). These two Devonian genera differ from the Visean heterocorals (whose microstructures were described by Lafuste 1981), because the elements which constitute the heterothecal walls in the Carboniferous forms show a marked curvature ("genicules" after Lafuste 1981) and also, they are broader than the Devonian microlamellae. It is impossible to attribute a phylogenetic significance to these differences due to insufficient knowledge of heterocorals microstructure.

The ultra-thin section examined contains skeletons of diverse organisms, whose microstructures are very well preserved (Fig. 10A, C). Among them, are bryozoans (fenestellids and some others) and tabulate corals (auloporids and striatoporids). Bryozoa, Tabulata and Heterocorallia mostly show distinct lamellar and microlamellar microstructures, with different dimensions, profiles and arrangements of microstructural elements for each group (Fig. 10A, C). The presence of such diverse microstructures in a single sample supports the hypothesis of a primary origin for all of them and, in consequence, their use as useful taxonomic characters (Tourneur et al. 1995).

External features: As previously mentioned, we only have at our disposal a single sample containing heterocorals embedded in their matrix (Fig. 8A). Nevertheless, some observations made from cross and longitudinal sections provide data on the possible external aspect of these corals.

They would have been long, thin, cylindrical, and slightly wavy corals (Figs. 5, 6). The upper part of the corallum would be formed by the septa, that is to say by the distal cone by Wrzołek (1981, 1993) and Karwowski and Wrzołek (1987). Directly below an area would exist composed of an initial tabulotheca, giving the corallite a stellate outline with septal crest and interseptal pockets, numbering from four to six of each. The outline of the septal crest would be gently curved, as produced by the microlamellae enveloping the free septal margins. The lowest part of the corallite would have more rounded appearance, as a result of the overlapping growth increments of the tabulotheca (Cossey 1997). Some features of the previously described structures could continue to appear locally.

The presence of trabeculae in the wall sclerenchyme of the heterocorals (if confirmed) may be evidenced by small spines or granules randomly sited over the external surface of the corallum (Fig. 9C, F). Should the development of fibres in the septal median plates be confirmed, as seems to be indicated by some of the observations made during this study, it would be possible to conclude that bigger or more developed granules would form concentrations around the areas of the coral that projected the most, that is, in vicinity of the septa.

Comparison and discussion

Stellaphyllia gen. nov. is characterized by great architectural simplicity and skeletal robustness, also in the coral's axial zone. Its affinities with the other pre-Famennian forms described to date cannot be precisely established because of the doubtful affinities of the latter (see paragraph "Supposed occurrences of Heterocorallia in the Middle Devonian"). However, the morphological appearance of the other supposed early heterocorals: *Pseudopetraia* Soshkina (a very elegant form with a well developed septal system) and *Tetraphyllia* Yoh et al. (with only four septa) is very different from *Stellaphyllia* gen. nov.

On the other hand, mature specimens of *Mariaephyllia* Fedorowski show an ample axial zone, with several generations of septa (Fig. 7D).

From the Famennian genus *Oligophylloides* Różkowska, *Stellaphyllia* gen. nov. can be clearly distinguished as the Famennian form is with marked difference between the narrow axial zone and the ample and compact peripheral rim, and by the different septal arrangement in the two forms (Fig. 7F).

Concerning the Carboniferous heterocorals, the great majority of specimens described as *Hexaphyllia* Stuckenberg or *Heterophyllia* McCoy are characterized by the presence of six septa (or some more in the case of *Heterophyllia*), but the thickening of the septa and the tabulotheca are, in each case, significantly lesser than those described in *Stellaphyllia* gen. nov. (Fig. 7E). Only one specimen, assigned by Semenoff-Tian-Chansky (1988: fig. 9) to *Heterophyllia* sp., from close to the Devonian/Carboniferous boundary at La Serre (Montaigne Noire, France), displays thickening and stellate forms similar to the specimens in the Spanish sample. Even so, this specimen has nine septa which reach the periphery of the coralla, and a diameter of 0.5 mm which is much smaller than the heterocorals described in this paper.

Given all the above, the forms described here cannot be assigned to any of the taxa described to date, and thus constitute a new genus and species.

Lifestyle

A detailed summary on the discussion concerning the lifestyle of the heterocorals can be found in Cossey (1997). Nevertheless and in spite of the numerous works, the mode of life of these strange corals remains quite unknown up to now.

Schindewolf (1941) inferred for the first time, the existence of an immature pseudoplanktic phase which could explain the wide paleogeographic distribution of some species. However, several lines of evidence suggest that all the heterocorals were benthic during their adult life, as proposed by

Cossey (1983). These arguments include: (1) occurrence of basal and lateral talons, spines and some other means of attaching themselves to hard surfaces, (2) occurrence of attached specimens, (3) fragile general morphology of the heterocorals and (4) occurrence of colonial heterocorals (Weyer 1995b). In addition, the geniculate or kinked corallites described by Cossey (1983, 1997) have been interpreted by this author as being corallites re-oriented themselves by settling unevenly in soft sediment (Cossey, 1997). This author also suggests that a benthic mode of life could explain the subtle morphological differences between two heterocoral populations coming from two different (an algal-reef and a fore reef) environments (Cossey, 1997).

There are no coralla bases among the material studied, and no cross sections have been found which would indicate anchorage structures. Nevertheless, one of the sections found shows a heterocoral overgrowing a bryozoan colony (Fig. 9E) which could, hypothetically, have provided a nucleus for attachment. This occurrence supports a benthic mode of life.

On the other hand, the trabecular spines or granules which appear on the external surface of *Stellaphyllia* are too small, and are in unsuitable positions to have served as neither a structure of cementation to various objects on the sea floor (Sugiyama 1984, 1989) nor for clinging on to any floating object as suggested by Schindewolf (1941).

Neither do they appear to have been sufficiently developed to have played a defensive function as has been suggested by Cossey (1995, 1997) for some spiny *Hexaphyllia* from the Lower Carboniferous in England. As occurs in *Stellaphyllia*, spines and tubercles described by Cossey (1997) appear to be continuous with the septa, but *Hexaphyllia* shows very numerous and quite long spines, which are distally curved in the direction of the corallite growth.

The function of these small spines in primitive heterocorals like *Stellaphyllia* remains unknown. These structures are the direct consequence of the septal growth beyond the tabulothecal wall and thus, their occurrence is related to the morphology and growth rate of the polyp. Given that most of the external surface of the corallite would have been covered by living tissue during life, an initial supporting function for the spine would not be rejected. This initial holding function would favour the positive selection and later development of long spines on stratigraphically younger corals like *Hexaphyllia,* in which a protective function for the spines would be effective.

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